

A field survey of the breeding habits of *Eretmodus cyanostictus*, a biparental mouthbrooding cichlid in Lake Tanganyika

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Synopsis

Oral incubation of young or 'mouthbrooding' reduces the selective advantages of care by two parents and thus biparental care is rare among 'mouthbrooding' fish. We surveyed the breeding biology of *Eretmodus cyanostictus*, a biparental mouthbrooder from Lake Tanganyika, to understand what factors maintain biparental care. We found larger males than females, a male-biased sex ratio and indications that spawning is synchronized around the full moon. These preliminary findings suggest that the benefits of desertion for males are low; males may maximize their reproductive success by helping raise young while females regain reproductive condition.

Introduction

In the majority of mouthbrooding cichlids, females provide parental care alone (Fryer & Iles 1972, Keenleyside 1991); biparental oral incubation is extremely rare. Out of an estimated 1000 species of mouthbrooding cichlids, only 35 provide biparental care (Breder & Rosen 1966, Oppenheimer 1970, Loiselle 1985, Keenleyside 1991, Kuwamura 1997). These biparental mouthbrooders are thought to represent an evolutionary transition between biparental substrate guarding species and uniparental mouthbrooding species (reviewed by Keenleyside 1991). Biparental care is often associated with the need for long-term co-defence of young and/or a breeding site (Barlow 1974, Clutton-Brock 1991). However, when the mouth is utilized as an incubation site, a small clutch can be protected effectively by one parent, thus reducing the selective advantages of biparental care. Furthermore, mouthbrooding

releases parents from long-term defence of a breeding site as the mouth can be used as a safe, mobile retreat for young (Gross & Sargent 1985, Barlow 1984, Keenleyside & Bietz 1981, Blumer 1979, 1985, Gittleman 1981). Thus biparental mouthbrooding is puzzling, and is commonly associated with large clutches that cannot fit into a single mouth cavity (Clutton-Brock 1991, Balshine-Earn 1995a, appendix E).

Here we report the results of a preliminary field study of the breeding biology of a biparental mouth brooder, *Eretmodus cyanostictus* (Boulenger, 1898), a little known cichlid from Lake Tanganyika. In *E. cyanostictus*, parents do not co-defend free swimming young and the entire clutch fits into a single parent's mouth. Females mouthbrood the eggs and embryos and then the male takes over the role until the young become independent (Kuwamura et al. 1989). Thus, neither large clutch size nor the need for co-defence of young explains biparental

care in this species. The factors that maintain biparental care, and in particular why males have not been emancipated from care (as in most mouth-brooding cichlids), remain unknown.

In general, biparental care is thought to be stable under the following evolutionary scenarios: (1) when the benefits of mate desertion are low, i.e., when the opportunity to remate is minimal (Barlow 1981); or (2) when the cost of mate desertion is high, for example, if both parents are necessary for successful territorial defense, incubation of eggs, feeding or defense of young (Barlow 1974, Perrone & Zaret 1979, Blumer 1985, Clutton-Brock 1991).

Our study had two principal aims. First, to investigate for the first time the breeding biology of *E. cyanostictus* from a population in the south of Lake Tanganyika. This species provides an interesting system to explore factors that may maintain biparental care (sex ratio, lunar cycles, ovarian synchronization). Thus our second aim was to examine the benefits and costs of desertion and so elucidate the selective forces that favour biparental care.

Materials and methods

This study was carried out between December 1996 and April 1997 at a site 4 km west of Mpulungu, Zambia, on the southern shore of Lake Tanganyika. We sampled fish found on approximately 100 m of shoreline between 0.5–9.0 metres depth. A Suunto dive computer was used to measure depth.

We captured fish on 25 separate occasions at different times of day and at different sites along the shore by laying a monofilament fence net (10 m long by 1.5 m deep with a mesh size of 10 mm) at 0.5 to 1.5 m depth. Using hand nets and snorkel equipment, fish were chased into the net. Only fish 4.5 cm standard length or larger were captured, as we were interested only in mature specimens. Captured fish were put into cages and then brought ashore in a bucket for sexing (by examination of genital papilla), measuring, and in some cases (fifty males and fifty females) dissection. Fish were killed using an overdose of the anaesthetic MS 222. All other fish were released at their collection points. Fifty males and fifty females were measured for weight

(to 0.01 g), standard length, total length, depth (from directly below the first spine of the dorsal fin), length of pelvic fins and length of the longest ray of the dorsal fin. A smaller sample of fish was also measured for nose length (N = 50) and mouth width (N = 63) (all measurements were taken using calipers, accurate to 0.1 cm). Mouth width was taken as the horizontal widest part of an open mouth.

To examine the pattern of ovarian maturation, females were caught over a period of eight weeks and their ovaries were removed, weighed (to 0.01 g) and classified into one of four categories: immature = 0 (small white oocytes, total weight < 0.01 g), unripe = 1 (mixture of small white and medium size orange oocytes, total weight 0.01–0.05 g), mature = 2 (mainly large orange oocytes, total weight 0.06–0.1 g), and ripe = 3 (very large orange oocytes, total weight \geq 0.1 g). Fish caught mouthbrooding were sexed and measured, and the number and size of the eggs or young were recorded. To determine the sex ratio, we recorded the total number of males and females found between 0.5 to 1.5 m depth on ten separate occasions in two weeks in March.

Results

Sexual dimorphism and sex ratio

There was clear sexual size dimorphism in our sample of *E. cyanostictus*; mature males were significantly larger (N = 50, mean weight \pm SE = 7.59 \pm 0.31 g, standard length \pm SE = 6.19 \pm 0.10 cm; depth \pm SE = 20.92 \pm 0.38 cm) than mature females (N = 50, mean weight = 5.03 \pm 0.16 g, standard length = 5.48 \pm 0.07 cm, depth = 18.28 \pm 0.25 cm). Kolmogorov Smirnov tests showed that males were larger (body weight $\chi^2 = 77.4$, $p < 0.001$; standard length, $\chi^2 = 77.4$, $p < 0.001$; body depth $\chi^2 = 77.4$, $p < 0.001$). We analysed the mouth, rostrum and fin measurements as covariates of standard length, using ANCOVA. Males had significantly larger mouths and longer pelvic fins than females. The adjusted mean mouth width (i.e. the mean after removing all differences that can be accounted for by standard length differences) was 7.95 and 6.53 mm for males and females, respectively (ANCOVA:

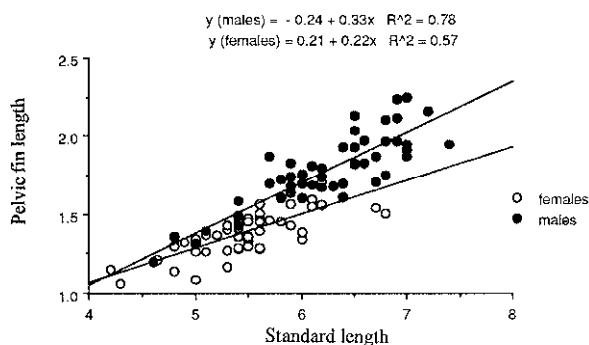


Figure 1. The allometric relation between standard length and pelvic fin length in males (●) and females (○).

$F_{(1,63)} = 5.18$, $p < 0.05$). The adjusted mean length of pelvic fin for males and females was 16.41 mm and 15.09 mm, respectively (ANCOVA: $F_{(1,97)} = 10.36$, $p < 0.01$: see Figure 1). There was no sexual dimorphism in dorsal fin size (ANCOVA: $F_{(1,97)} = 0.35$, $p = 0.55$) or rostrum length (ANCOVA: $F_{(1,50)} = 1.23$, $p = 0.27$). In the field, *E. cyanostictus* is an olive brown colour with striking sky-blue spots, but showed no obvious sexual dichromatism. In total we caught 101 males and 72 females; nine of the ten samples were male biased (binomial test (2 tailed): $N = 10$, $p = 0.01$).

Ovary maturation and mouth brooding

The mean ovary weight was 0.08 g and it correlated positively with body weight (Pearson $r = 0.43$, $p < 0.05$). The pattern of ovarian maturation during the study period did not show any synchronization (Figure 2). Many Tanganyikan cichlids show lunar synchronization of spawning (Nakai et al. 1990). To determine if this was true for *E. cyanostictus*, we lumped the ovary categories 0 and 1 as 'immature' and categories 2 and 3 as 'mature' and examined whether ovaries matured in relation to the lunar cycle. For one week on either side of new moon we found 20 immature and 13 mature ovaries. For one week on either side of full moon we found 15 immature and 14 mature ovaries. This pattern is not different from what would be expected if eggs matured at random (Chi squared test; $\chi^2 = 0.53$, $N = 52$, $p < 0.30$); thus ovary maturation appeared to be asynchronous with respect to lunar cycling.

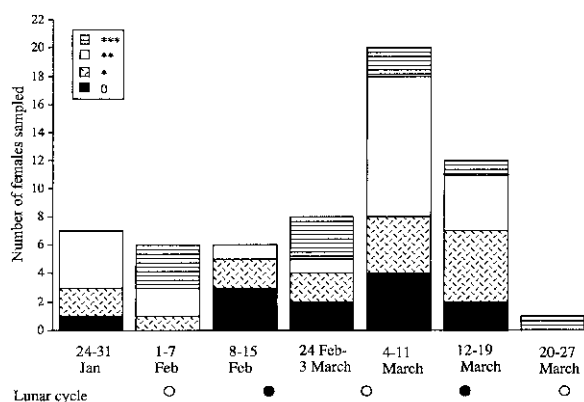


Figure 2. The categories of ovary maturation by weeks throughout the study period. All stages were usually found in each week (0 black bars = immature; * white hatched bars = unripe; ** white bars = mature, and *** black hatched bars = ripe). The open circles refer to the full moon and filled circles refer to the new moon.

In contrast, mouthbrooding in males and females was consistent with a scenario of lunar cycle synchrony. Only three males were found to be mouthbrooding in the period of one week on either side of new moon, whereas 13 males and females were found to be mouthbrooding during one week on either side of full moon, a significant departure from the random null hypothesis (Chi squared test; $\chi^2 = 6.2$, $N = 16$, $p = 0.01$). All five female mouthbrooders were caught within the six days following full moon.

Number of young and size in relation to mouth brooding parent

The median number of young or eggs found in female mouthbrooders was 15 (range 9–18, $N = 4$). One of the female mouthbrooders had eggs and the others had newly hatched young. The median length of young found in females was 5.9 mm (range 4.5–7.5 mm total length). The median number of young found in males was 11 (range 7–20, $N = 9$) and the median young length was 9.7 mm total length (range 6.5–12.4 mm). Thus males had more developed young, supporting the hypothesis that females transfer young to males. We found no correlation between mean young size and number ($r_s = -0.39$, $N = 12$, $p = 0.21$).

Behavioural observations

Mating was observed just prior to full moon (22 Dec 1996; M. Taborsky personal communication); it was prolonged (> 40 min) with regular interruptions and occurred on flat, sheltered rock. Prior to oral pick-up of the orange eggs that are released one at a time, the female nuzzled and gently butted the male's genitalia, suggesting buccal fertilization. In the laboratory, females incubate the eggs and then young in their mouths for 10 to 15 days before they are transferred into the male's mouth for another 10–16 days of care (B. Taborsky personal communication). We never observed parents defending free swimming young.

Discussion

This study indicates that *E. cyanostictus* practices female-to-male shift mouthbrooding; both females and males care for offspring, as reported in a study of this species from the north of Lake Tanganyika (Kuwamura et al. 1989). The female broods eggs and then passes on parental duties to the male. This, combined with our field observations that pairs defend territories together, suggests that the species is monogamous. We found that *E. cyanostictus* is sexually dimorphic for body size, lives in male-biased populations and seems to mate around full moon.

Biparental mouthbrooding is believed to be an evolutionary transitional state between biparental substrate guarding and uniparental mouthbrooding (Lowe McConnell 1959, Fryer & Iles 1972, Barlow 1974, Keenleyside 1979, Peters & Berns 1982). Several hypotheses that have been suggested to explain why biparental care is maintained may apply to the goby-like cichlids (tribe Eretmodini). First, biparental care may be maintained by the need for pair defense of free swimming young (Barlow 1984). However, we never observed joint defense of mobile young against predators in the field and furthermore captive parents are not observed to care after they release young from their mouths (Kuwamura et al. 1989, J. Morley & B. Taborsky personal communication). Second, biparental care might

be maintained as a result of the need for pair defense of a feeding territory (Kuwamura 1986, Kuwamura et al. 1989). Feeding habits and distribution of food, however, are not thought to have a strong effect on parental care patterns among cichlids (Barlow 1974, Kuwamura 1997). While we cannot reject this hypothesis, it seems unlikely from comparative evidence. Among the closely related goby-like cichlids (Eretmodini), the insectivorous *Tanganicodus irsacae* and the herbivorous *E. cyanostictus* (Yamaoka et al. 1986) are biparental mouthbrooders whereas another herbivorous species *Spathodus marlieri* is a maternal mouthbrooder (Kuwamura et al. 1989). Third, biparental care may be maintained by monogamy: if a pair breeds repeatedly then paternal contribution and partial emancipation of the female from parental duties will increase the reproductive success of the pair (Yanagisawa 1986, Kuwamura 1997). Our results provide partial support for this third hypothesis.

We found a male-biased sex ratio and synchronous mouthbrooding (spawning), suggesting that males will have few additional mating opportunities if they desert. From work on a related species of goby cichlid, we know that females are capable of caring for eggs and young on their own (Kuwamura et al. 1989). However, by caring and partially reducing their female's care period, the male allows her to recover faster and lay eggs again more quickly (Loiselle & Barlow 1978, Balshine-Earn 1995b). Thus, by not deserting, males may be maximizing their own reproductive rate as well as that of their mate's.

Females may spawn at full moon to improve the probability of young surviving. One tilapine species from the Ethiop River in Nigeria and eight species of lamprologines from Lake Tanganyika show lunar synchronization of spawning (Schwanck 1987, Nakai et al. 1990). Lunar synchronization is thought to be important because at full moon light improves nocturnal guarding of eggs and minimal night light, two weeks later (new moon) may provide better cover for young dispersal. However, moonlight is unlikely to be important for *E. cyanostictus*. Eggs are well protected in the mouth cavity so moonlight is not necessary for guarding. In addition, as young are incubated for approximately one month (see

above) they would emerge at full moon, and would not have the advantage of darkness for dispersal. Alternatively, by synchronizing spawning behaviour females might effectively force males to stay put, since deserting males would have to wait for the next full moon to mate again. Once males are committed to remain with one female, by providing care a male can increase his reproductive rate by reducing his partner's inter-clutch interval (as argued above). We propose that *E. cyanostictus* females use the full moon as a cue to synchronize spawning in order to ensure male parental care.

The male-biased sex ratio may have reflected a true sex bias in the shallow surge zone of the lake, via differential mortality or male-biased primary sex ratio (Clutton-Brock & Parker 1995). Alternatively, the observed male biased sex ratio may have been a sampling artifact. Our results show that males were larger than females, which might make them more obvious and therefore easier to catch (which could bias the observed sex ratio). In addition, if males are more active and take more risks (as in many other species, McKay 1991) then it is possible that males were more susceptible to capture.

Both the male biased sex ratio and the lunar synchronization of spawning reduce mating opportunities for males, so they may benefit more by relieving females from care, reducing the time until the next eggs are ovulated. Since our sample sizes are small, our conclusions concerning the adaptive significance of biparental care in *E. cyanostictus* must be considered tentative. Our study highlights the need for further work on biparental mouthbrooding in general and in eretomidine cichlids in particular.

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